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Exceptional Pleistocene vermetid crusts preserved in a cave located 130 m a.s.l. near Taormina (NE Sicily)

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SHORT TITLE: Vermetid crusts from a raised Pleistocene semi-submerged cave

KEY WORDS: Bioconstructions, morphological adaptations, shell structure, semi-submerged caves, dating, Neotectonics.

ABSTRACT – Wide coastal sectors of north-eastern Sicily are shaped by strong Pleistocene tectonic activity of the area and concurrent glacio-eustatic sea level changes leading to the formation of terraces, characterised by basal marine sediments topped by continental vertebrate-bearing sediments, and of caves with evidences of marine submersion. A tidal notch and associated organogenic crusts formed by the vermetid gastropod *Dendropoma petraeum* found in a cave near Taormina, located at an elevation of 130 m a.s.l., just above the terrace produced during the Tyrrhenian (MIS 5.5), were examined. This represents the first record of extensive vermetid bioconstructions inside a cave, as well as of a particular morphology of *D. petraeum* shells, which include coiled initial parts and straight distal elongated parts, with numerous internal septa. These specimens were preserved in a restricted area, with elongated parts aligned parallel to each other and facing downward from a sub-horizontal step along a wall. The location of the vermetid crusts and the particular ecological requirements of this species (presently forming bioconstructions in exposed rocky shores characterised by high light and water energy) points to a cave which was semi-submerged and widely open to the sea currents at the time of its colonisation. The particular *Dendropoma* shell morphology has been interpreted as an adaptation to reach penetrating water currents more rich in food and oxygen, also seen in other organisms from cave habitats. The U-Th dating of *Dendropoma* shells and the cementing continental calcite crust produces apparent ages that are not consistent with the stratigraphic position of the cave, and are significantly younger than expected. As observed for other dating results on the same species (and other molluscs), this indicates an alteration of the system during diagenesis and suggests caution in the use of certain species as stratigraphic constraints.

RIASSUNTO - [Eccezionali croste di vermetidi pleistocenici conservate in una grotta sollevata a 130 s.l.m. presso Taormina (Sicilia)] – Ampi settori costieri della Sicilia nord-orientale sono stati modellati dall'interazione fra l'intensa tettonica prevalentemente verticale dell'area, che ha comportato considerevoli sollevamenti durante il Pleistocene, e la concomitante azione dei ripetuti cambiamenti del livello del mare verificatisi nello stesso intervallo temporale, che hanno causato la formazione di diversi ordini di terrazzi oltre a morfologie erosive come i solchi di battente, nonché la formazione/ampliamento di grotte costiere. I terrazzi, correlabili a livello regionale, sono caratterizzati da depositi marini di ambienti superficiali, alla base, e sormontati da depositi continentali contenenti resti di vertebrati.

Il più ampio terrazzo, denominato "Po" ed esteso tra le quote di 150 e 60 m, è un terrazzo policiclico che include due piattaforme di abrasione i cui margini interni sono ubicati alle quote di 130 e 100 m s.l.m.. I depositi marini soprastanti alla piattaforma di abrasione di quota 100 m sono stati attribuiti al MIS 5.5 per la presenza di *Persististrombus latus*. In questo contesto, in una grotta attualmente alla quota di 130 m s.l.m., appena più alta del terrazzo tirreniano, è stato descritto un solco di battente associato con croste formate

dal gasteropode vermetide Dendropoma petraeum, estese diversi m² e spesse solitamente un paio di centimetri. Sebbene di spessore limitato, questa è la prima segnalazione all'interno di una grotta di una vera e propria biocostruzione prodotta da questo vermetide che solitamente è stato riscontrato in questi ambienti solo con esemplari isolati. Tenuto conto che D. petraeum forma attualmente biocostruzioni in ambienti costieri rocciosi aperti in condizioni di elevata illuminazione e di alta energia idrodinamica, il ritrovamento di estese incrostazioni di questa specie suggerisce che almeno la porzione di grotta in cui esse sono presenti fosse ampiamente aperta verso l'esterno al momento della sua colonizzazione, ipotesi abbastanza congruente con le elevate dimensioni dell'ingresso. Molto interessante è anche la particolare morfologia che questi gasteropodi sviluppano in una ristretta area, lungo una porzione suborizzontale, a gradino, della parete settentrionale della grotta. Qui le conchiglie di D. petraeum sono avvolte solo inizialmente ma sviluppano successivamente lunghe porzioni distali erette e lievemente ondulate addossate le une alle altre e rivolte verso il basso. Queste lunghe porzioni erette non sono assimilabili a "feeding tubes" o tubi temporanei per l'alimentazione, per la loro continuità con la parte avvolta della conchiglia. Inoltre, diversi setti sono presenti al loro interno, indicando che si trattava di conchiglie persistenti all'interno delle quali i molluschi continuavano a vivere, con il corpo alloggiato in posizioni progressivamente più distali. In analogia con quanto osservato in altre grotte e per altri gruppi di organismi, questa particolare morfologia è stata interpretata come funzionale a raggiungere correnti di acqua che fluivano dall'esterno, presumibilmente ricche di particelle nutritive e in ossigeno. La datazione effettuata col metodo dell'Uranio-Torio su conchiglie di D. petraeum ha dato risultati non congruenti con la contestualizzazione temporale derivante dalle indicazioni stratigrafiche. L'età apparente, decisamente più giovane di quella attesa, indica che il sistema è stato alterato durante la diagenesi, probabilmente a causa della elevata porosità tipica delle biocostruzioni a vermetidi. Scostamenti dello stesso ordine dimensionale, ottenuti sempre datando conchiglie di D. petraeum (oltre che di altri molluschi), suggeriscono cautela nel loro impiego e consigliano ulteriori verifiche, anche in vista della possibile compilazione di una lista di specie non impiegabili a questo scopo.

INTRODUCTION

Terraced marine and continental deposits, as well as cave deposits have been described by Bonfiglio (1981) in the Taormina area, north-eastern Sicily (Fig. 1). In this context, a cave located close to the ancient Greek theatre, at an altitude of 130 m a. s. l., preserves conglomerates, as well as a barely visible marine notch locally perforated by *Lithodomus* boreholes and coated by vermetid crusts. In a first description of the vermetid crust, Bonfiglio et al. (2015) highlighted this finding as unusual. Indeed, in the present day Mediterranean Sea, gregarious vermetid gastropods construct three-dimensional structures with different morphologies but are invariably reported from rocky coasts located at or immediately below sea level, in settings exposed to a considerable water energy, because of the requirement for nutrition and respiration (Safriel, 1975; Antonioli et al., 1999; Chemello & Silenzi, 2011).

In this paper, the Taormina cave is reconsidered, focusing on: 1) a new detailed mapping of the cave and its vermetid encrustations; 2) a geobiological description and interpretation of the unusual vermetid bioconstructions found inside the cave and their possible contribution to the understanding of raised Pleistocene coastlines of the area; 3) an attempt to provide geochronological constraints on the formation of vermetid encrustations, using U-Th methods.

MARINE TERRACES AND CAVES IN THE MESOZOIC CARBONATE ROCKS OF TAORMINA AREA

The oldest paper dealing with Taormina terraces and coastlines is that of Dominici (1922), but Toschi (1936) gave the first detailed description of marine terraces and uplifted Holocene marine notches of the area.

Terraces are morphological features consisting of a planar surface gently inclined seawards and bounded by scarps, both uphill and downhill. In the study area, numerous marine terraces have

formed as the result of the interaction between the general intense long-term uplift trend affecting north-eastern Sicily and the Messina Straits since early-middle Pleistocene to Holocene times, and the Pleistocene glacio-eustatic changes of the sea level. Each terrace is correlated with a glacio-eustatic high sea level represented by odd numbers in the marine isotopic record. The geological structure of a terrace includes different elements, which have been originated through the geological processes occurring in the uplifted regions. An abrasion surface and overlying marine and continental sedimentary cover are present.

The widest terrace of north-eastern Sicily, named "Grand replat" by Hugonie (1979) and "Po" by Catalano & De Guidi (2003), is located between 150 and 60 m a.s.l., and extends from Cape Peloro to Acquadolci to the west, and to Taormina, along the Ionian coast, to the south. It has been used as a key terrace for regional terrace correlation in north-eastern Sicily (Robillard, 1975; Hugonie, 1979; Bonfiglio, 1987). The "Po" terrace (Fig. 2) consists of polycyclic marine deposits including two distinct abrasion surfaces, named I (inner edge at about 130 m a.s.l.) and II (inner edge at about 100 m a.s.l.).

At Cape Peloro, Bonfiglio & Violanti (1983) described the sedimentary cover of the abrasion platform II, that is located between 100 and 80 m a. s. l., which is composed of marine sands containing *Persististrombus latus* (Gmelin, 1791), first reported as *Strombus bubonius* Lamarck, 1822. This species is the clear palaeontological evidence for the last interglacial highstand in the Mediterranean, pointing to the marine isotope substage MIS 5.5, corresponding to the stage 5e in the deep-sea $\delta^{18}\text{O}$ isotopic record. Palaeontological analyses of molluscs collected at +105 m in a fossiliferous marine conglomerate at Taormina, part of the sedimentary body of the abrasion platform II, indicate that the sea was a few metres deep when these deposits formed (Antonioli et al., 2006). An imprecise age of 124.5 ± 15.0 ka has been obtained based on ESR methodology applied to *Patella* and *Venerupis* shells, and the terrace has been attributed to MIS 5, and probably to MIS 5.5 substage by Antonioli et al. (2006). Abrasion platform I, that is at greater altitude and presumed to be older, has not been dated so far.

Terraces recognised in the Taormina area are reported in Fig. 3. The profile A–A' shows the 180–220 terrace (the terrace around the Greek theatre and on which the town of Taormina is built), the 90–120 terrace (attributed to the MIS 5.5 substage by Antonioli et al., 2006) and a younger terrace at 30–60 m a.s.l. The 140–160 terrace is present north of Taormina (profile B–B') but is lacking east of the A–A' profile, where some caves open on the steep cliff of hard-resistant carbonate rocks. Several of these caves contain remains of Pleistocene mammals (*Cervus elaphus siciliae* Pohlig, 1893), *Hippopotamus pentlandi* von Mayer, 1832 and *Palaeoloxodon*, probably *Palaeoloxodon* sp. nov. of Herridge (2010).

The age of colonization of the cave, now at an elevation of 130 m, by the vermetid gastropod *Dendropoma petraeum* remains an open question and could have been during any one of a number of preceding Quaternary high sea stands. Also, taxonomic/palaeoecological analyses of the gastropods are still open questions, which have been addressed in the present paper.

METHODS

The location and height of the cave in relation to present-day sea level was measured with a GPS device. A survey was carried out to measure the floor extension and estimate the height of the ceiling in the different cave sectors. Photographs were taken at appropriate sites to reconstruct the general morphology and record the locations of the main physical and geobiological features.

The biogenic crust, consisting of vermetid gastropods occurring inside the cave, was carefully investigated *in situ* and photo-documented. Sampling was minimised to conserve the natural heritage offered by the cave, also in view of a possible exploitation for large public in the future. Samples, collected at the time of the first investigation of the Taormina Cave in the early 1980s (Bonfiglio, 1981) were reanalysed at the Palaeoecological Laboratory of the University of Catania, using a Zeiss V8 stereomicroscope for species identification. Selected shell fragments were

examined uncoated with a scanning electron microscope (Tescan Vega LMU) in low vacuum conditions using back-scattered electrons at the Microscopical Laboratory of the University of Catania.

In the absence of any other suitable material for dating, such as corals, speleothems, ash layers etc., we attempted to determine the U-Th age of the vermetid shells and coating, fully aware that such material is rarely successful because of its susceptibility to post-depositional addition or loss of U and Th. Vermetid shell fragments showing a double-layered structure pointing to preservation of the pristine mineralisation, locally including the nacreous aspect, were picked for U-Th dating. Material from the secondary calcite coating/mould was carefully separated from shell fragments. Each sub-sample was treated with minimal abrasive cleaning, etched in dilute hydrochloric acid and ultrasonicated in distilled water.

An attempt to constrain the age of the deposit was made by standard U-Th methods for carbonate materials. The analytical methods employed were broadly similar to those described in Hoffmann et al. (2007), although U and Th separation was conducted using UTEVA resin. Samples were dissolved in HNO₃, spiked with ²²⁹Th/²³⁶U tracer prior to separation. U and Th isotopic ratios were determined by multi-collector inductively-coupled mass spectrometry (Thermo Neptune) at the University of Bristol using sample-standard bracketing protocols. All ages and isotopic ratios are quoted at the 2-sigma level.

RESULTS

Cave map and its morphological features

The present-day appearance of the cave is the result of a long frequentation by visitors. Remains of an Upper Palaeolithic soil overlaying the sterile conglomerate are still preserved in some inner cave portions (Bonfiglio, 1981). Humans repeatedly used the cave, even in historical times, as also indicated by the occurrence of artefacts, essentially located in its larger and most external part, just behind the entrance.

The cave has developed along a fracture line. It opens in the southwest-facing slope of the Cape Taormina promontory through an ogival entrance nearly 7 m wide at its base and 8 m high in its central part. The maximum length and width of the unique subterranean space are about 23 m and 8 m, respectively (Figs 4, 5).

The cave consists of a wide near-entrance chamber and a more irregularly-shaped inner sector (Figs 4, 5). The near-entrance main chamber is about 7 m long and maintains roughly the same cross section morphology and dimensions of the opening for almost all its length. In contrast, the inner sector bifurcates as the result of a 2 m wide rocky pillar longitudinally elongated inside the cave, leaving only narrow passages near the blind end. The height of this internal sector is much lower, usually not exceeding 2 m and only reaching 3.7 m at the junction with the main chamber. The decrease in height observed going inwards depends on both ceiling lowering and the ascending cave floor, which is widely covered by polymictic conglomerates and a calcite crust of subaerial precipitation. This continental calcite crust coats the surface of the conglomerate, binding together the pebbles and the rare cobbles forming its topmost layer, but also drapes large portions of the walls, forming stalactite- and stalagmite-like structures lining the rock pillar.

The rock is only locally exposed along the pavement, which is also covered by soil immediately beyond the entrance, but largely visible along the ceiling and the walls. A sea cave notch (Carobene, 2015) is evident along the walls and particularly in the inner sector, less than 1 m above the present-day calcite-coated conglomerate. Partly-eroded *Lithophaga* boreholes are barely visible in restricted portions of this notch in the innermost recesses of the cave.

Invertebrate evidence: the vermetid crust

A biogenic crust occurs inside the cave, only detected in the middle part of the walls, between about 7 and 10 m from the entrance (Fig. 5).

Although boundaries between the biogenic crusts and the rock are difficult to distinguish, it seems that, at least in this sector, the crust extends vertically for about 1.8 m, reaching a maximum altitude of about 2.5 m above present-day cave floor.

The biogenic crust is formed by vermetid gastropods, but its appearance varies greatly within the cave. The biological encrustation is nearly continuous along the southern wall, where 1-2 cm thick superficial slabs have been locally found adherent to the rock. These slabs largely consist of coiled vermetid moulds and, rarely, poorly preserved skeletal material embedded in a carbonate crust (Fig. 6a). Nevertheless, for its main extension, the crust occurrence is merely indicated by the presence of subcircular-to-irregularly-shaped, often clustered, holes, measuring 2-3 mm in diameter, which point to embedded vermetid specimens (Fig. 6b).

Along the northern cave wall, the biogenic crust is more discontinuously preserved and usually indicated by clusters of holes. A sample of crust (6x7 cm wide and more than 4 cm thick) with these external features (Fig. 6c) detached from a prominent surface sector revealed the presence of superimposed vermetid specimens (Fig. 6d) forming a solid elevated framework. Along the same wall, at about 9 m from the entrance, a prominent rock overhang forms a roughly planar step nearly 1.5 m long and 50 cm wide, where the vermetid crust reaches a thickness of 10 cm (Figs 7a, b). Close inspection shows that only the initial portions of *Dendropoma* shells are coiled whereas the downward-facing adult teleoconch portions are elongated and lean closely to each other in a gently wavy pattern (Fig. 7b). Shells are closely packed and show septa inside the tubular cavities (Fig. 7), which are empty with only the lumen surfaces coated by tiny calcite crystals, or completely to partly filled by lithified sediment which also occurs in interspaces between shells (Figs 7c-h). Within adult specimens, areas are present filled by clustered juveniles sometimes delivering larval shells useful to identify the specimens as belonging to *Dendropoma cristatum* (Biondi, 1859) (Rosso et al., 2016). Microscopical observation revealed the preservation of fine morphological shell features, such as the external ornamentation. Although some specimens show evidences of decalcification, most shells are still preserved with their pristine mineralisation and the concentric layering of the mesostracum indicating subsequent growth increments. Scanning electron microscopy of shell sections revealed their complex structure including layering and the aragonite crossed lamellar structure of the intermediate shell layer (Fig. 8).

U/Th dating of vermetid shells and calcite coating

Uranium concentrations for the *Dendropoma* shell and calcite coating were 0.93 and 1.87 $\mu\text{g g}^{-1}$, respectively. Th concentrations were low $< 10 \text{ ng g}^{-1}$ and indicative of minimal detrital contamination. U-Th dating of *Dendropoma* shells gave an age of $72 \pm 0.9 \text{ ka}$ (2s), which is much younger than expected from morphological and stratigraphic evidence in the area (Tab. 1). The calcite crusts that coated the vermetids, and presumably immediately above it, are indicative of precipitation during continental settings, and yielded ages somewhat older, around $78.5 \pm 0.9 \text{ ka}$. U isotopic data is useful because it can indicate the extent to which a marine signal has been preserved. The $^{234}\text{U}/^{238}\text{U}$ initial activity ratio for the shell and coating are 1.274 ± 0.003 and 1.179 ± 0.002 , respectively. Modern sea water has a value of 1.145.

DISCUSSION

The apparent age of the cave in the framework of the terrace sequence

The value obtained for the initial $^{234}\text{U}/^{238}\text{U}$ activity ratio was higher than that (1.145) expected for closed-system behaviour of pristine vermetids with U co-precipitated in the shells in equilibrium with sea water. One might expect fossil shells to have a value similar to that of modern sea water because the ratio in ocean waters has changed very little ($< 1\%$) over glacial-interglacial cycles

because of the long residence time of U (Dunk et al., 2002) (see Chutcharavan et al., 2018 for review). An elevated, initial U-activity ratio suggests alteration of the system by groundwater during diagenesis after the shells emerged above sea level, potentially by the same waters that produced the calcite coating. This would give an erroneous apparent age. The same sort of problems were revealed in a study carried out in Sardinia by Carboni et al. (2014). These authors found that ages obtained from dating of vermetid specimens (and a second mollusk, also) were significantly different from those obtained for associated scleractinian *Cladocora coespitosa* (Linnaeus, 1767). These apparent ages are inconsistent with, and about 50 ka younger than those inferred from the co-occurrence of "Senegalese faunas" in the same layers as confirmed by further geochronological and lithostratigraphic data (Carboni et al., 2014). This difference is very similar to that obtained from dating of *Dendropoma* specimens of the Taormina Cave, given the stratigraphic position of the cave within the terrace series observed in the Taormina area. This striking similarity in bias reinforces the expectation of poor reliability of using vermetid shells for chronological constraints, but further systematic studies would be desirable to elucidate possible causes of the consistent bias. For Sardinian vermetids, weak cementation and porosity have been indicated as possible causes for U addition, that is usually typical of early diagenetic phases (Carboni et al., 2014). Indeed, it must be remarked that high porosity is widespread in the Taormina material also, and it is inherent to vermetid bioconstruction and directly linked to the large (up to about 3 mm in diameter and 3-4 cm in length) cavities, that remain inside the tubular skeletons after the animals' death. Consequently, it could be expected that skeletons of these organisms cannot be used or must be used with caution for dating purposes. The same has been suggested for the bivalve *Lithophaga lithophaga* (Linnaeus, 1758) by Rowe et al. (2015) and the construction of a list of species not fully suitable for dating purposes, is here suggested.

Ages of the vermetid crust (72 ± 0.9 ka) and the superimposed inorganic calcite precipitation (78.5 ± 0.9 ka), although similar, are stratigraphically reversed. A combination of the high degree of porosity and surface area associated with the tube cavities, which are currently empty of sediments, and the susceptibility of aragonite to alteration could account for this anomaly. Open system conditions may have persisted in this bioconstruction and allowed continuous U uptake. For the continental calcite coating, we can make no a priori assumptions about the U isotopic composition. The apparent age for this material of ~ 79 ka may be the true mean age, but additional consistent results at higher spatial resolution would be required to provide a more robust constraint and this was not feasible here.

The vermetid community

Vermetids are known to inhabit present-day and fossil cave habitats. Nevertheless, only a few species have been reported, among which mostly *Serpulorbis arenaria* Linnaeus, 1767 (see Cattaneo-Vietti, 2003). Rare records pertain to *Petalconchus glomeratus* (Linnaeus, 1758) (Accademia Cave, Ustica southern Tyrrhenian Sea: Di Geronimo et al., 1997), and to undetermined species (Plemmirio caves, south-eastern Sicily: Sanfilippo et al., 2015). Analogously, vermetids from fossil, mostly Pleistocene, submarine caves include *Petalconchus intortus* (Lamarck, 1818) (Fulco Cave, north-eastern Sicily: Rosso et al., 2017) and two vermetid species (Rumena Cave, western Sicily: Rosso et al., 2015), possibly *P. glomeratus* and *Dendropoma granulatus* (Gravenhorst, 1831) (Antonietta Rosso and Rossana Sanfilippo, unpublished data).

What is of interest here is that, within both fossil and present-day submarine caves, vermetids (including *Dendropoma*) have been recorded as isolated specimens, interspersed in between other benthic organisms (see literature reported above). Surprisingly, however, in the Taormina cave *D. cristatum*, first reported as *D. petraeum* (Monterosato, 1884) (Bonfiglio, 1981), forms dense populations of closely-spaced individuals preserved in the cave as an extensive crust of nearly 6 m² wide, and 1 to 10 cm thick.

Possessing an encrusting aragonite skeleton and being a highly gregarious species, *D. cristatum* is able to actively form 'build-ups' in lower mesolittoral and shallow infralittoral rocky

settings in the present-day Mediterranean Sea in association with the non-geniculate coralline alga *Neogoniolithon brassica-florida* (see Pérès & Picard, 1964; Safriel, 1975; Chemello, 2009; Chemello & Silenzi, 2011; Donnarumma et al., 2018). Interestingly, the main core of the build-ups develops along the margin of exposed rocky coasts, where up to > 1 km long, >40 cm wide and 50 cm thick 3-D structures can form. These structures actively grow, offering microhabitats for rich and diversified organism associations, colonising crevices (Chemello et al., 1998; Chemello, 2009; Chemello & Silenzi, 2011). Discontinuous, smaller and thinner crusts, <50 cm wide and <5 cm in thickness, characteristically form landwards along the inner margin of the few-metres wide intertidal rocky platforms (Chemello & Silenzi, 2011) and in sheltered sites (Donnarumma et al., 2018). The occurrence of *Dendropoma* bioconstructions and their development and thickness depend on i) the presence of suitable lithotypes among which calcarenites and limestones seem to be the best, although some contrasting evidences have been reported (see Schiaparelli et al., 2003; Donnarumma et al., 2018); and ii) by local exposure, with high hydrodynamic energy enhancing the growth and the extension of the build-up (Chemello & Silenzi, 2011; Donnarumma et al., 2018) and its elevation in relation to sea level (Rovere et al., 2015; Donnarumma et al. 2018). The observed thickness of the Mediterranean *Dendropoma* reefs results from the equilibrium between biogenic construction and mechanical and biological destruction and has been achieved roughly in the last 2000 years, when vermetid growth established at, or close to, the present-day sea level, following the decrease in speed of sea-level rise during the present interglacial phase (Silenzi et al., 2004). Somewhat similar bioconstructions, formed by an unidentified *Dendropoma* species, are known from the Pliocene of NE Spain (Aguirre et al., 2014), presumably developed at comparable depths on coastal morphological heights.

Considering all of the above, the occurrence of extensive, although relatively thin, crusts along the walls of a semi-submerged cave is extremely unusual because no modern analogues have been observed to the knowledge of the authors, at least in the Mediterranean area (Renato Chemello, personal communication, May 2015). Taking into account the ecological requirements of present-day populations of *D. cristatum*, it could be suggested that the cave was a site of relatively high hydrodynamic energy, at least comparable to that reaching the inner margin of vermetid platforms, allowing the formation of thin vermetid rims nowadays (see above). The high light intensity required by present-day *Dendropoma* buildups to grow, was presumably, at least partly, ensured by light penetration allowed by the width of the cave opening and its exposition. Indeed, at the time of vermetid colonization, the cave was partly flooded by the sea during a highstand, and the opening, exposed to the south-east, was about 6-7 m wide and 5 m high, at least in its central part. Consequently, incoming light was presumably enough for *Dendropoma* to grow, at least in the bigger and more external chamber where crusts have been found. However, it could be hypothesised that the crust remained thin, presumably, because of the relatively unfavourable environmental conditions, although further constraints (including time of exposure to suitable conditions) cannot be ruled out (see below). Unlike present-day *Dendropoma* buildups, the absence of usually associated coralline algae and fauna is noteworthy. Explanations could be searched for in possible particular environmental conditions, which occurred within the Taormina cave allowing vermetid colonisation but seemingly excluding further, less tolerant and more light-dependent, organisms. It is worth noting the dramatic reduction in the cover of the calcareous alga *N. brassica-florida* on vermetid bioconstructions located in the infralittoral fringe (< 30 cm deep) in respect to those of the upper mesolittoral, found by Donnarumma et al. (2018) along the Tyrrhenian coast of Campania. No trace of any organism, such as corals, serpulids, bryozoans, brachiopods or sponges, usually forming rich associations within submarine caves (i.e. Zibrowius, 1978; 1995; Harmelin, 1986, 2000; Balduzzi & Rosso, 2003; Bianchi & Sanfilippo, 2003; Pisera & Vacelet, 2011; Gerovasileiou & Voultsiadou, 2012; Rosso et al., 2013a, b; 2015; 2017; 2018; Guido et al., 2017; Sanfilippo et al., 2017) has been found. However, owing to the current lack of information about any vermetid community from present-day submarine caves, hypotheses about environmental conditions favouring their formation would remain purely speculative..

Traces of the boring bivalve *L. lithophaga* were not associated with vermetids but only restricted to small areas in the inner recesses of the cave. Holes are incomplete perhaps because the rock they were produced in was later partly eroded or they were produced at least partly in an unpreserved biogenic crust like in the Rumena cave (Rosso et al., 2015) dated to the Lower Pleistocene (Stocchi et al., 2017). The nature of this possible crust remains unknown but was presumably formed by more easily detachable/less preservable skeletonised epibionts. In any case, the location of the vermetid crusts and *Lithophaga* boreholes, whose vertical distributions nowadays largely overlap (see Rovere et al., 2015) consistently point to a sea level reaching an altitude of about 2 m above the present-day cave floor. It is likely that sea level remained at this height for only a short period because the observed crust is thin, usually < 2 cm thick and hence consisting of only few superimposed vermetid generations. Even where the crust is 10 cm thick, it is largely formed by a single to few generations of *Dendropoma* specimens, and most of the thickness corresponds to the elongate teleoconch terminations of their shells, set side by side, although few younger specimens may grow on the older ones.

The observed morphology, including a coiled initial portion followed by a long uncoiled tubular portion, is strange within vermetids, as well. Vermetid shells usually consist of three morphologically and functionally distinct parts (Schiaparelli & Cattaneo-Vietti, 1999) including the 1) first coils separated from the rest of the shell by internal septa, followed by 2) the protective shell coils, sturdy attached to the substratum and 3) occasionally by temporary feeding tubes, which allow a reorientation of the aperture. These last parts are straight, with a wall that is thinner in relation to the rest of the tube, more or less elongate, and usually not cemented to the substratum. Nevertheless, possibly because of the strong water motion of the habitat, *D. cristatum* has been observed to produce no feeding tubes (Schiaparelli & Cattaneo-Vietti, 1999). Indeed, the uncoiled shell portions (Fig. 7b) of *Dendropoma* specimens colonising the inverted step along the northern side of the Taormina cave do not share any of their features with feeding tubes as described for vermetids other than *Dendropoma*. The shell is thick and formed by a succession of perfectly concentric layers pointing to a symmetrical construction of the shell and not to a bending obtained through asymmetrically-constructed thin shell increments. Furthermore, several internal septa are present all along these portions indicating that they were not temporary structures. Instead, these uncoiled shell portions were permanent and the animals lived inside them, and what's more, *Dendropoma* specimens progressively shifted their bodies in new "chambers" they obtained cutting off the rest of the shell with the backward insertion of a new septum. The production of such uncoiled partitioned shell portions has never been reported for *Dendropoma* or other vermetids. Straight elongated isoriented shell portions have been reported for *Petalochonchus* populations from the Messinian of a Salento locality in southern Apulia, by Vescogni et al. (2008). Those tubes are otherwise only superficially similar to those of *Dendropoma* from the Taormina cave, because they are decidedly straight and not contiguous to each other. They have been interpreted as feeding tubes and no detailed description is given, possibly taking into account that erect portions are well known for the genus *Petalochonchus*. Furthermore, the Messinian *Petalochonchus* specimens, contributed to form a "reef" in slope settings, and grew upwards, unlike those observed in the Taormina cave. Here, the growth is downward directed and elongation appears clearly functional to ensure the animals a position farther from the rocky sub-horizontal inverted step of the cave wall where specimens first settled. In the absence of other organisms with which to compete, it could be suggested that this special adaptation could have been driven by the scarcity of food supply inside the cave and the need to go far from the colonised rocky substratum to reach the main stream of water flow. The same strategy (including the hanging down and the elongation of body, and skeleton) seems to be exploited by both colonial and gregarious organisms belonging to different taxonomic groups in cave environments (and also overhangs) both in the past and present. Key examples include corals and crinoids from the Devonian of Morocco (Jakubowicz et al., 2013);

hanging elongated coral colonies of *Astroides calycularis* (Esper, 1794) of a filled cave of Tyrrhenian age in NE Sicily (Rosso et al., 2017); the living *Desmophyllum* corals in 28 m deep overhangs from Chile (Föster et al., 2005); living and dead specimens of the serpulid *Protula* from caves of Apulia (Belmonte et al., 2009), SE Sicily (Sanfilippo et al., 2015), and the Aegean Sea (Sanfilippo et al., 2017; Guido et al., 2017), as well as the freshwater serpulid *Marifugia cavatica* Absolon and Hrabě, 1930, from Crnulja cave in Hercegovina (Kuprianova et al., 2009) whose numerous and straight contiguous tubes strongly recall *Dendropoma* bioconstructions from the Taormina cave.

CONCLUSIONS

The Taormina cave, with its interesting and well-preserved fossil record, adds to the few known examples of well-documented past submarine caves with fossil biological encrustations. All these caves are located in tectonically-active areas, the Fulco and the Taormina caves in the north-eastern corner of Sicily (Rosso et al., 2017 and present paper, respectively) and the Cape Vagia cave in Rhodes (Steinthorsdottir & Håkansson, 2017). Bioerosions and/or encrustations were sometimes already known from the same caves (Bonfiglio, 1981; Bromley & Asgaard, 1993, respectively for the last two caves), but only in recent years they are being recognised as records of cave palaeocommunities and past habitats at or close to the sea level at the time of their growth. As expected from knowledge on the present day cave communities, and although partly biased by diagenesis, these palaeocommunities point to high heterogeneity between caves, largely deriving from different morphologies, geographical and bathymetrical location (constraining environmental parameters), and possibly composition of neighbouring biota during colonisation time.

The Taormina cave, presently observed at an altitude of 130 m a.s.l., preserves a surprising fossil community that freezes a time of its geological history, when it was partly submerged and widely open to the sea. The separation of areas with *Lithophaga* boreholes in the inner recesses of the cave, and of *Dendropoma petreum* crusts in the outer, near-entrance sector, points to a gradient of relevant environmental parameters, such as light and hydrodynamic energy, within the palaeocave. The relevant width of the cave entrance and its exposure along the palaeocoast could have allowed the co-occurrence, at least near the cave opening, of high light intensity and water energy, enough to ensure suitable conditions for the settlement, growth and maintenance of *D. petreum* populations. This species, presently forming "reef" habitats at sea-level in exposed rocky shores, is first reported from cave environments not with isolated specimens but as a builder able to form extensive crusts of densely-packed superimposed specimens. Furthermore, within this unusual and particular habitat, a high plasticity has been documented for the first time for this species, able to form downward-facing clusters of specimens developing elongated, raised, uncoiled terminal shell portions, with frequent internal septa allowing the animal to live close to the shell orifice. Like for other taxonomic groups of organisms, it has been suggested that the elongation of the shell and elevation from the substratum is functional to project the animal within the main water-flow bringing oxygen and food, mainly from the outside.

The preservation of vermetid 'reefs' in the fossil record is extremely rare (see above). Even present-day bioconstructions are prone to dismantlement caused by the same water energy that is needed for their development, when it becomes very high. Consequently, the finding of the vermetid crusts in the Taormina cave was presumably allowed by the relatively sheltered habitat but also favoured by deposition of the conglomerate sediments still present on large sectors of the cave floor and sealed by the subsequent subaerial calcite precipitation.

Results of dating attempts using *Dendropoma* shells are significantly different from expectations based upon geometric and stratigraphic position of the organogenic vermetid crusts, which are probably associated with high sea-level stands older than MIS 5. We confirm previous concerns about the use of these gastropods, and more widely, of molluscs as chronological constraints using

U-Th methods. Further investigations are required to explain the difference between expected and apparent ages and if this shift is systematic and could be corrected for. We encourage others to reveal alternative examples, in addition to *Dendropoma* species and *L. lithophaga*, that promote caution in use for geochronology.

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CAPTIONS

Tab. 1. U, Th concentrations and isotopic ratios (analytical uncertainty is 2 sigma).

$[^{230}\text{Th}/^{238}\text{U}]_{\text{activity}} = 1 - e^{-\lambda_{230}T} + (\delta^{234}\text{U}_{\text{measured}}/1000)[\lambda_{230}/(\lambda_{230} - \lambda_{234})](1 - e^{-(\lambda_{230} - \lambda_{234})T})$, where T is the age. Decay constants are $9.1577 \times 10^{-6} \text{ yr}^{-1}$ for ^{230}Th , $2.826 \times 10^{-6} \text{ yr}^{-1}$ for ^{234}U , and $1.55125 \times 10^{-10} \text{ yr}^{-1}$ for ^{238}U . The degree of detrital ^{230}Th contamination is indicated by the measured $[^{230}\text{Th}/^{232}\text{Th}]$ activity ratio. Age corrections were calculated using $^{232}\text{Th}/^{238}\text{U}$ activity ratio = 0.746.

Fig. 1. The study area within the Mediterranean (a) and in the north-eastern corner of Sicily (b).

Fig. 2. Oversimplified outline of the geological structure of the polycyclic "Po" terrace recorded from north-eastern Sicily. I and II abrasion platforms and overlying sedimentary bodies made up by beach gravels (bottom) and vertebrate-bearing deposits (top). Open circles: *Lithodomus* boreholes (modified from Bonfiglio et al., 2010).

Fig. 3. The Taormina terraces and caves. a) map showing the position of the studied cave (asterisk) in relation to terraces recognized in the region: 1, 2 and 3, placed at 220-180, 160-140, 120-90 m a.s.l., respectively. The terrace at 60-30 m a.s.l. (unnumbered) is also shown. Large open circle: Taormina; small black circles: further caves; A-A'; B-B': traces of the profiles in b; b) idealized section (exaggerated heights) to show the location of the Taormina Cave in relation to terraces. c) original scheme of the Taormina Cave. Modified from Bonfiglio (1981 and Bonfiglio et al. (2010).

Fig. 4. The Taormina Cave morphology. a) general view from the entrance showing the central pillar and the bifurcating inner side; b) the southern side of the cave from the inside showing the step formed by conglomerates locally preserved below continental calcite crusts (short arrow) and a bare notch (long arrow); and c) close-up of the conglomerates still cemented and covered by the continental crust (on the left) and dismantled (on the right), against the blind termination of the cave. The arrow indicates the tidal notch.

Fig. 5. Map of the Taormina Cave. a) Plant view with the indication of transversal (A-A', B-B' and C-C') and longitudinal (D-D') sections, reported in b) and c), respectively. All symbols are reported in the figure.

Fig. 6. *Dendropoma cristatum* (Biondi, 1859) from the Taormina Cave. a-b) views of the surface of the southern wall of the Taormina cave, at nearly 2 m from the present-day cave floor: a) at about 6 m from the entrance, exposing small holes corresponding to the *D. cristatum* apertures, scale bar: 2 cm; b) at about 7 m from the entrance showing *D. cristatum* internal moulds after dissolution of the skeletons, scale bar: 2 cm; c-d) detail of a sample collected along the northern wall, at about 8 m from the entrance: c) exposed surface, scale bar: 1 cm; d) surface cut sub-parallel to the exposed one showing well preserved vermetid shells, partly filled by sediment, scale bar: 1 cm.

Fig. 7. *Dendropoma cristatum* (Biondi, 1859) from the Taormina Cave and details of its elongated shells. a) a step-like overhang along the northern side of the cave, at about 9 m from the entrance, showing a thick crust of closely spaced *D. cristatum* specimens with particularly long, downward facing terminal shell portions, scale bar: 10 cm; b) detail of a) to show the closely spaced, elongated, uncoiled terminal vermetid shell portions, scale bar: 1 cm. c-i) general views and details of a small collected sample. c) lateral view showing undulating tubular shell portions, scale bar: 1 cm; d) view of the detached surface showing contiguous tubular portions, some cross-sections disclosing internal septa with the convexity first oriented towards the rocky step, scale bar: 1 cm; e) a different lateral section with nearly straight and closely contiguous tubes, scale bar: 1 cm; f) section of a tube portion from the basal part of c) to show internal septa, scale bar: 5 mm; g) tubular shell with two closely-spaced subsequent septa. Note the layered tube walls, scale bar: 5 mm; h) close-up of d) to show internal septa, scale bar: 5 mm; i) young *Dendropoma* specimens with coiled shells in the interspaces between elongated straight tubes, scale bar: 5 mm.

Fig. 8. Shell structure of *Dendropoma cristatum* (Biondi, 1859) from the Taormina Cave. a) inclined section (inner tube at the bottom) showing the main tube and the complex stacking pattern of imbricate external laminae (top), scale bar: 200 μm ; b) close-up of the central sector in a) showing the aragonite crossed lamellar structure of the intermediate shell layer and some laminae, scale bar: 50 μm .